MycoKeys

MycoKeys 109: 171–185 (2024)
DOI: 10.3897/mycokeys.109.133879

Research Article

Two new species of *Pholiota* (Agaricales, Strophariaceae) from the southwest of China

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Abstract

Two new mushroom species from Southwest China, *Pholiota cylindrospora* and *P. subterrestris*, are described in this study. *Pholiota cylindrospora* is characterized by its dry pileus with slightly recurved and triangular scales, cylindrical basidiospores, and two types of pleurocystidia—leptocystidia and chrysocystidia—as well as its growth on soil. *Pholiota subterrestris* is identified by a brownish-orange pileus with numerous brown fibrillose scales; pale brown lamellae with even edges; a stipe covered with recurved fibrillose scales; elliptical spores with a distinct but small germ pore; and pleurocystidia containing typical amorphous refractive inclusions of chrysocystidia. Both species are described and illustrated, and a phylogenetic analysis of a multigene dataset (ITS + 28S) is presented. Morphological and phylogenetic analyses confirm that *P. cylindrospora* and *P. subterrestris* are distinct from the other *Pholiota* species, and both belong to the subgenus *Pholiota*. A key to the species of subgenus *Pholiota* from China is provided.

Key words: Chrysocystidia, morphology, phylogeny, Subgenus *Pholiota*, taxonomy

OPEN ACCESS

Academic editor: María P. Martín
Received: 4 August 2024
Accepted: 5 September 2024
Published: 8 October 2024

Citation: Huang J-h, Lei C-y, Shen Y-l, Tian E-j (2024) Two new species of *Pholiota* (Agaricales, Strophariaceae) from the southwest of China. MycoKeys 109: 171–185. https://doi.org/10.3897/mycokeys.109.133879

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Introduction

Pholiota (Fr.) P. Kumm. is distributed worldwide, especially in the northern temperate zone, and currently contains approximately 150–160 species (Smith and Hesler 1968; Jacobsson 1991; Holec 2001; Kirk et al. 2008; Noordeloos 2011; Holec et al. 2014; He et al. 2019; Liu et al. 2024). Species of this genus grow on wood, sawdust, humus, soil, or, more rarely, on sphagnum beds or charcoal (Smith and Hesler 1968; Jacobsson 1991). Most *Pholiota* species are saprotrophic, and a few are parasitic (Holec 2001). Some species of this genus are edible and medicinal, such as *P. adiposa* (Batsch) P. Kumm. and *P. aurivella* (Batsch) P. Kumm. (Smith and Hesler 1968; Wu et al. 2019). However, this genus also contains mildly toxic species (Smith and Hesler 1968; Wu et al. 2019).

Pholiota is an important and stable genus of the family Strophariaceae. Nevertheless, its previously proposed infrageneric classification systems vary owing to differing concepts of the genus, from as many as seven subgenera to three (Singer 1962; Smith and Hesler 1968; Singer 1975; Jacobsson 1991; Holec 2001; Noordeloos 2011). Tian and Matheny (2021) proposed that *Pholiota* sensu stricto comprises at least two major subgenera, Subgen.

Pholiota and Subgen. *Flammuloides*, although several residual poorly placed lineages were also noted, depending on the dataset analyzed in the study. The subgenus *Pholiota* is stable in different infrageneric taxonomic systems of the genus *Pholiota*. The subgenus *Pholiota* is mainly characterized by pileus and stipe with distinct scales, as well as chrysocystidia or very similar sterile cells in the hymenium of many of the species (Smith and Hesler 1968; Holec 2001). Approximately 62 species of *Pholiota* have been reported in China, including 12 species belonging to the subgenus *Pholiota* (Mao and Jiang 1993; Tian and Bau 2004; Bau et al. 2005; Tian and Bau 2011a, 2011b; Tian et al. 2016; Liu et al. 2024).

This study discovered two new species from the Southwest of China, belonging to subgenus *Pholiota*, based on morphological examination and phylogenetic analyses. The results are presented in the following sections.

Materials and methods

Morphological studies

Fresh specimens were collected from Southwest China and deposited at the Herbarium of Mycology of Jilin Agricultural University (HMJAU) in Changchun City, China. The specimens were documented using color descriptions from Kornerup and Wanscher (1978) and then dried on dehydrators. The dried specimens were examined in 5% KOH solution, and the dextrinoid reactions were tested using Melzer's reagent (Singer 1986).

Basidiospores were measured and examined according to the methods of Tian and Matheny (2021) and Tian et al. (2021). Line drawings of the microstructures were obtained from the rehydrated samples.

Abbreviations: "L" denotes the number of lamellae extending to the stipe; "l" indicates the number of lamellae between each adjacent pair; "Q" represents the length/breadth ratio of basidiospores; "Q_m" refers to the mean value of "Q" measurements across all studied collections ± the sample standard deviation.

DNA extraction, PCR, and data set assembly

DNA was extracted from 10 to 20 mg of ground, dried basidiome tissue using a Plant Genomic DNA Kit (Tiangen Biotech Co., Ltd, Beijing). The internal transcribed spacer region (ITS) of Nuc rDNA was amplified and sequenced using the primers ITS1 (TCCGTAGGTGAACCTGCGG) and ITS4 (TCCTCCGCTTATTGATATGC) (White et al. 1990; Gardes and Bruns 1993). The 28S rDNA ribosomal region was amplified and sequenced using the primers LR0R (GTACCCGCTGAACTTAAGC) and LR7 (TACTACCACCAAGATCT) (Vilgalys and Hester 1990). The DNA sequences generated in this study were deposited in GenBank. A two-locus dataset (ITS+28S) was assembled using AliView 1.28 (Larsson 2014). The sequences generated in this study were merged with the partial multigene dataset from Tian and Matheny (2021). The ITS+28S dataset was constructed using representative *Pholiota* species, including 36 type collections. *Stropharia* species were selected as outgroups, based on Tian and Matheny (2021). Information on the sequences used in this study is shown in Table 1.

Table 1. Specimen data and DNA sequences analyzed in this study.

Species	Specimen-voucher (Herbarium)	Origin	GenBank accession numbers	
			ITS	28S
Pholiota adiposa	ET37 (HMJAU37520)	China, Jilin	MN209721	MN251112
P. agglutinata	AHS60691 (TENN-F-028806, isotype)	USA, Idaho	MN149356	MN251113
P. aurivella	CBS 262.32	Netherlands	MH855317	–
P. aurivella	SJ84131	Sweden	AF195603	–
P. aurivella	ET27 (HMJAU37516)	China, Jilin	MN209728	MN251116
P. aurivella	ET42 (HMJAU37521)	China, Jilin	MN209729	MN251117
P. aurivella	ET19 (HMJAU37425)	China, Inner Mongolia	MN209771	MN251154
P. avellaneifolia	AHS59589 (TENN-F-028809 isotype)	USA, Idaho	MN209731	MN251120
P. baeosperma	TFB7383 (TENN-F-054431)	Chile	MG735312	–
P. baeosperma	RHP8315 (TENN-F-054993)	Argentina	KY559332	–
P. baptistii	ET542 TENN-F-028810 (isotype)	USA, Idaho	MN149364	–
P. brunnescens	AHS3525 (MICH 11657, holotype)	USA, Oregon	MG735292	–
P. brunnescens	PBM3057 (TENN-F-063855)	USA, California	MG735314	–
P. caespitosa	TENN-F-015908 (holotype)	USA, Tennessee	NR119908	–
P. carbonaria	AHS9500 (MICH 11663, holotype)	USA, California	MG735288	–
P. castanea	DPL7769 (TENN 071878)	USA, Texas	MH016952	–
P. castanea	TENN 020269 (holotype)	USA, Tennessee	HQ222025	–
P. chocenensis	PRM 895066 (holotype)	Czech Republic	NR_155622	–
P. conissans	SJ96017, FCUG1273	Sweden	AF195606	–
P. conissans	CBS 175.47	France	MH856205	–
P. conissans	CBS 243.50	France	MH856603	–
P. conissans	voucher 395	Italy	JF908575	–
P. conissans	voucher 6610	Italy	JF908581	–
P. cylindrospora	**ET-Ti2(holotype)**	**China, Yunnan**	**PQ013666**	**PQ013732**
P. cylindrospora	**ET-yun2**	**China, Yunnan**	**PQ013686**	**PQ013733**
P. decorata	AHS54770 (TENN-F-028816)	USA, Idaho	MN209734	–
P. ferrugineolutescens	TENN-F-028807 (isotype)	USA, California	HQ222026	–
P. flavescens	TENN-F-01309) (isotype)	USA, Tennessee	MN209735	MN251124
P. fulviconica	LRH28818 (TENN-F-028818)	USA, Idaho	MN209738	MN251126
P. fulviconica	AHS65898 (TENN-F-028820, isotype)	USA, Idaho	MN209739	MN251127
P. fulvozonata	AHS73887 (MICH 5316, holotype)	USA, Idaho	MG735290	–
P. gallica	PRM 933232	France	LN889967	–
P. gallica	MPU 3478 (holotype)	France	HG007988	–
P. gummosa	SJ84095, FCUG1254	Sweden	AF195605	–
P. gummos	CBS 216.39	Portugal	MH855985	–
P. gummos	CBS 210.48	Portugal	MH856313	–
P. highlandensis	NYS 1468.1 (isotype)	USA, New York	MH016956	–
P. highlandensis	PBM4085 (TENN-F-071544)	USA, Tennessee	MG735310	–
P. humii	AHS58633 (TENN-F-028822, isotype)	USA, Idaho	MN209740	MN251128
P. jahnii	SJ83118, FCUG1061	Sweden	AF195604	–
P. kodiakensis	TENN-F-028804 (isotype)	USA, Alaska	MN149360	–
P. lenta	ET33 (HMJAU37519)	China, Jilin	MN209742	MN251130
P. lenta	PBM4233 (TENN-F-074640)	USA, N. Carolina	MN209743	MN251131
P. limonella	ET28 (HMJAU37345)	China, Inner Mongolia	MN209747	MN251135

Species	Specimen-voucher (Herbarium)	Origin	GenBank accession numbers	
			ITS	28S
P. limonella	MF68025 (TENN-F-074669)	USA, Tennessee	MN209748	MN251136
P. limonella	ET11 (HMJAU37362)	China, Jilin	MN209741	MN251129
P. limonella	ET13 (HMJAU37514)	China, Jilin	MN209746	MN251134
P. lubrica	ET29 (HMJAU37517)	China, Jilin	MN209751	MN251139
P. lubrica	ET4 (HMJAU22678)	China, Jilin	MN209753	MN251141
P. lundbergii	LL950724	Sweden	AF195607	–
P. lurida	AHS66386 (TENN-F- 028770, isotype)	USA, Michigan	MN209757	–
P. luteobadia	AHS43222 (MICH 11688, holotype)	USA, Michigan	MG735289	–
P. marangania	HLepp856 (CANB 574576)	Australia	MG735320	–
P. melliodora	AHS68780 (TENN-F-028861, paratype)	USA, Oregon	MN209758	–
P. mixta	SJ96022	Sweden	AF195609	–
P. mixta	PBM2499 (TENN-F-062357)	USA, Mass.	MH016953	–
P. molesta	AHS65008 (TENN-F-028830, isotype)	USA, Idaho	MG735296	–
P. molesta	JFA9246 (WTU 10719)	USA, Washington	MG735297	–
P. multicingulata	PBM3587 (TENN-F-066655)	Australia	MN209760	–
P. multicingulata	ET23 (HMJAU37414)	China, Yunnan	MN209761	MN251146
P. nameko	ET7 (HMJAU37512 / TENN-F-074767)	China, Jilin	MN209762	MN251147
P. nameko	ET10 (HMJAU22620 as *Pholiota* "*microspora*")	China, Jilin	MN209759	MN251145
P. occidentalis	AHS58470 (TENN-F-028874, paratype)	USA, Idaho	MN209765	MN251150
P. olivaceodisca	TENN-F-017778 (holotype)	USA, Tennessee	NR119909	–
P. olivaceophylla	MICH 290502 (holotype)	USA, CA	KF878381	–
P. parvula	AHS42234 (TENN-F-028834, isotype)	USA, Michigan	MN149362	–
P. polychroa	PBM2866 (TENN-F-062649)	USA, Louisiana	MG735317	–
P. prolixa	AHS5027 (TENN-F-028838, isotype)	USA, Michigan	MN209766	–
P. rubronigra	AHS56192 (TENN-F-028840, isotype)	USA, California	MH016955	–
P. rufodisca	B925 (TENN-F-028869, paratype)	USA, New Mexico	MN209767	–
P. sp.	ET38 (HMJAU22691)	China, Jilin	MN209737	MN251125
P. spumosa	ET12 (HMJAU37513)	China, Jilin	MN209776	MN251159
P. spumosa	LRH12950 (TENN-F-012950	USA, Tennessee	MN149361	–
P. squarrosa	PBM2735 (TENN-F-062547)	USA, Colorado	DQ494683	DQ470818
P. squarrosa	AH-48188	Spain	MF345959	–
P. squarrosa	SFC20140912-I01	South Korea	KX773886	–
P. squarrosa	Voucher 28	Germany	FR686575	–
P. squarrosa	ET26 (HMJAU37515)	China, Jilin	MN209777	MN251160
P. squarrosa	ET15 (HMJAU37366)	China, Jilin	MN209778	MN251161
P. squarrosoides	TENN-F-061728	USA, Tennessee	FJ596877	–
P. squarrosoides	SFC20120814-45	South Korea	KX773887	–
P. squarrosoides	JACA-MICO-00132	Spain	MF345957	–
P. squarrosoides	TENN-F-061692	USA, N. Carolina	FJ596860	–
P. squarrosoides	AH-48186	France	MF345958	–
P. stratosa	AHS64684 (TENN-F-028845, isotype)	USA, Michigan	MN209779	–
P. subsaponacea	AHS74095 (MICH 5332, holotype)	USA, Idaho	MG735287	–
P. subterrestris	**ET-072240 (holotype)**	**China, Guizhou**	**PQ013700**	**PQ013730**
P. subterrestris	**ET-gui2**	**China, Guizhou**	**PQ013701**	**PQ013731**
P. tennesseensis	TENN-F-018848 (holotype)	USA, Tennessee	NR_119910	–

Species	Specimen-voucher (Herbarium)	Origin	GenBank accession numbers	
			ITS	28S
P. terrestris	RAS371 (TENN-F-074807)	USA, Tennessee	MN209781	–
P. terrestris	iNat62825743	USA,New York	OP681747	–
P. terrestris	iNat62849835	USA,New York	MW644574	–
P. tetonensis	WGS3763 (TENN-F-028849, isotype)	USA, Wyoming	MN149367	–
P. velaglutinosa	AHS9285 (TENN-F-028851, isotype)	USA, Oregon	MH016954	–
P. virescens	HMJAU22498 (holotype)	China, Jilin	JF961378	–
P. virescentifolia	TENN-F-020591 (holotype)	USA, Tennessee	NR_119911	–
P. virgata	B763 (TENN-F-028832, paratype)	USA, New Mexico	MN209782	–
Stropharia acanthostipitata	CA01222011 (TENN-F-071898)	Dominican Republic	MG735313	–
S. acanthostipitata	JBSD 127401(holotype)	Dominican Republic	NR_156637	MF882994
S. rugosoannulata	X-31	USA	KC176328	–

Note: DNA sequences generated in this study are in bold.

Phylogenetic analysis

Bayesian Inference (BI) analysis was conducted using MrBayes 3.2.7 (Ronquist et al. 2012). Maximum Likelihood (ML) and bootstrap analyses were performed in RAxML 8.2.9 (Stamatakis 2014). GTR+I+G was selected as the best-fit model for the datasets using jModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012). One thousand bootstrap replicates were performed in ML analysis for the dataset. Two million generations were run in the BI analysis using four chains and other default parameters for the dataset, sampling trees, and other parameters every 1000 generations. Trees sampled from the first 25% of generations were discarded as burn-in, by which point the average standard deviation of the split frequencies had reached < 0.01. After the BI analysis, the potential scale reduction factors (PSRFs) were approximately 1.0 for all parameters. The Bayesian Posterior Probabilities (BPPs) were then calculated. Alignments of the datasets were submitted to TreeBASE (31577).

Results

Phylogeny

Eight new sequences (four ITS and four 28S) from the two species were produced in this study (Table 1). The dataset (ITS+28S) consisted of 59 taxa (36 type collections) and 2922 sites, all of which were included before analyses. The phylogram, with branch lengths inferred from MrBayes including support values (PPs and bootstraps) from both BI and ML, is shown in Fig. 1. The ML analysis produced nearly identical estimates of the topology to those of BI.

In the phylogram (Fig. 1), the representative *Pholiota* species and type collections were gathered together with strong support (PP = 1, BP = 100), and two major clades were inferred: the Subgenus *Pholiota* clade and the Subgenus *Flammuloides* clade. The two new species described here, *P. cylindrospora* and *P. subterrestris*, clustered within the Subgenus *Pholiota* and represented relatively independent lineages.

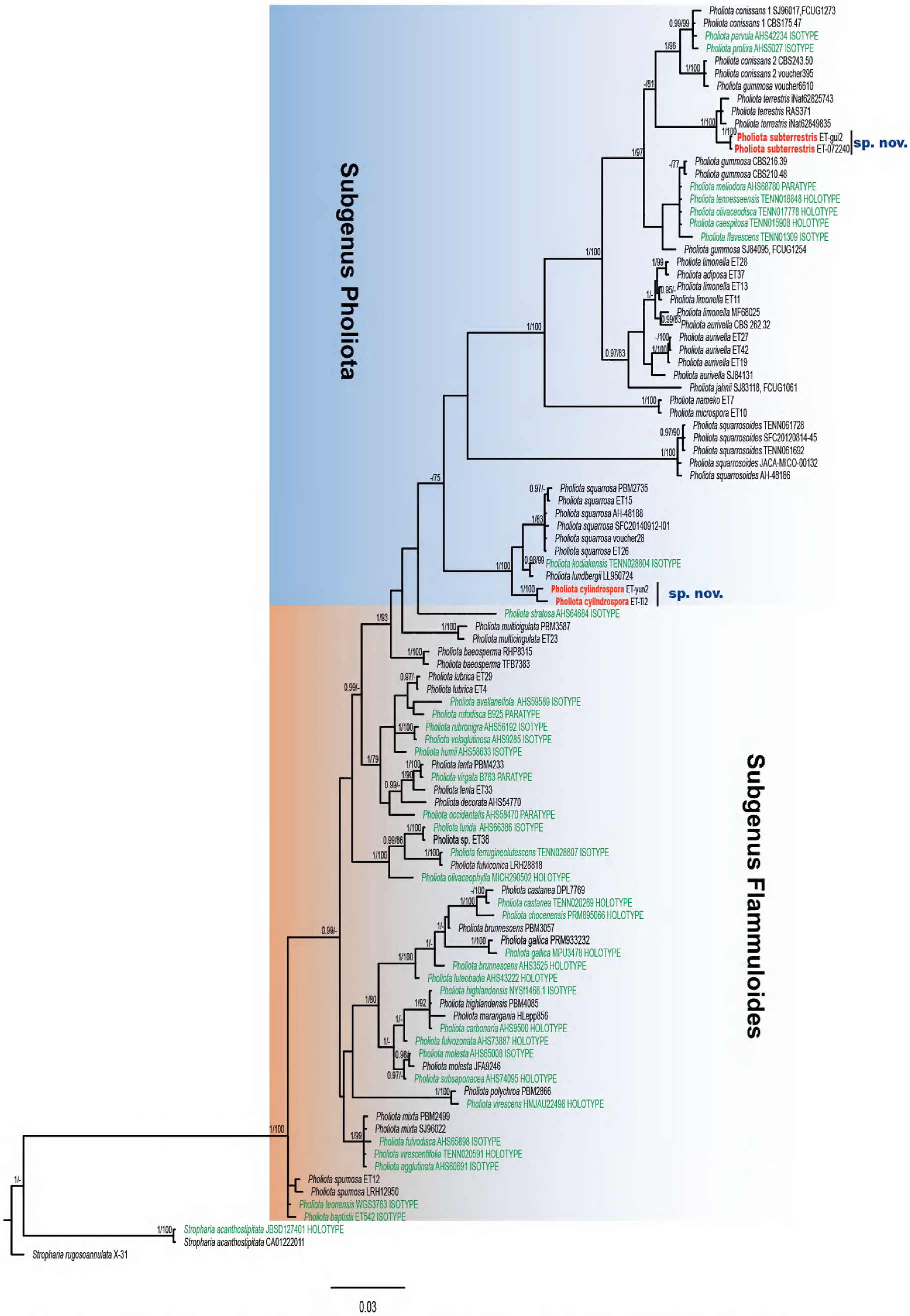

Figure 1. BI phylogram of *Pholiota* based on the dataset (ITS+28S). PPs > 0.95 and bootstrap values > 70% are shown. Types are indicated in green, and the new species from China in this study are in red.

Taxonomy

Pholiota cylindrospora **E.J. Tian, sp. nov.**
MycoBank No: 854827
Figs 2, 3

Diagnosis. Differs from other *Pholiota* species by dry pileus with slightly recurved and triangular scales, cylindrical basidiospores, and two types of pleurocystidia, including leptocystidia and chrysocystidia, as well as growing on soil.

Holotype. China. • Yunnan, Baoshan City, Gaoligong Mountains, Baihualing; elev. 910 m; 25°03'33"N, 98°49'18"E; scattered on soil in broad-leaved forest; 30 November 2015; Shi-liang Liu 37432 (holotype: HMJAU!).

Etymology. Referring to the cylindric basidiospores.

Description. ***Pileus*** 50–70 mm in diameter, convex to broadly convex, becoming nearly plane, with a low obtuse umbo; surface dry, pale orange to apricot (5A3–5B6), paler towards the margin, decorated with concentric, slightly recurved, triangular, light brown (6D7) scales. ***Context*** pale (2A2), odor and taste mild. ***Lamellae*** adnate, broad, moderately close, L = 38–42, l = 2–6, pallid at first, becoming brown (6D6), the edges waved. ***Stipe*** 45–60 mm long, 8–11 mm thick, central, equal to tapered towards the base, solid, ground color pallid, smooth to silky above an annular zone, towards the base with yellowish brown to brown (5D6–6D6) multizonate squamules or sometimes with scattered brown (6D5) fibrils, with white mycelium at the base.

Figure 2. Basidiomata of *Pholiota cylindrospora* (HMJAU37432, holotype). Photo by Shi-liang Liu. Scale bar: 1 cm.

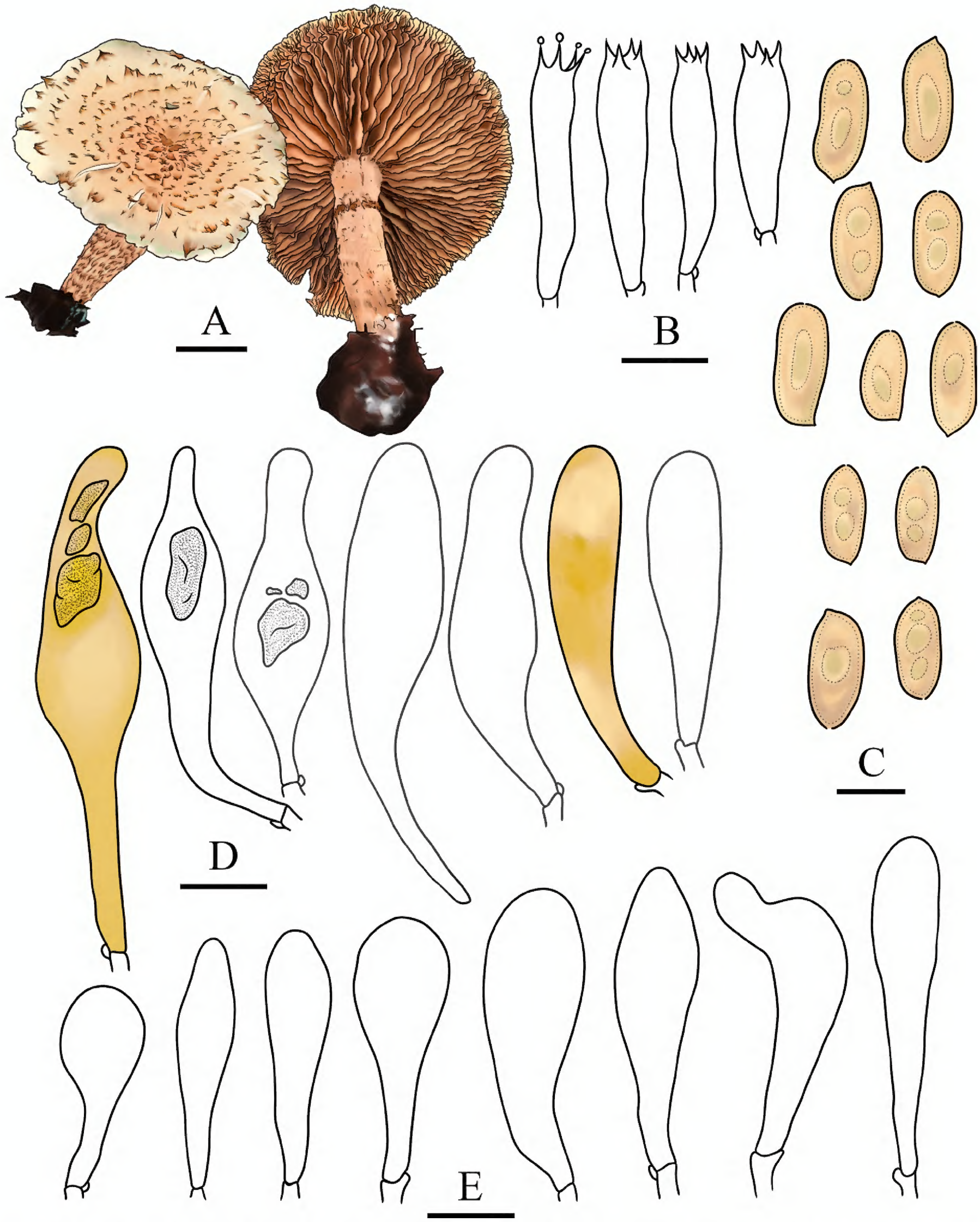

Figure 3. Microcharacters of *Pholiota cylindrospora* (HMJAU37432, holotype). Drawings by Jia-hui Huang **A** basidiocarps **B** basidia **C** basidiospores **D** pleurocystidia **E** cheilocystidia. Scale bars: 1 cm (**A**); 5 µm (**C**); 10 µm (**B**, **D**, **E**).

Basidiospores (6.5–)7.0–9.5(–10.0) × 3.0–4.0 µm, Q = 1.75–2.83, Q_m = 2.30, in face view oblong to cylindric, sometimes crooked, in profile cylindric to slightly inequilateral, wall smooth and thin, germ pore very minute to not evident, pale rusty to yellowish brown (6E8–5E8) in KOH, slightly paler in Melzer's reagent. ***Basidia*** 19–27 × 4.9–6.5 µm, 4-spored, clavate, hyaline in KOH. ***Pleurocystidia*** of two types: 1) leptocystidia, 35–55 × 8.5–10 µm,

clavate to subfusoid, thin-walled, smooth, content homogeneous, hyaline to pale yellowish brown to brownish (5D5–5E7) in KOH; 2) chrysocystidia, 39–60 × 9.5–12.5 µm, lageniform to clavate with a rostrate to mucronate apex, rarely forked near the apex, with an amorphous highly refractive inclusion, pale rusty to yellowish brown (6E8–5D5) in KOH. ***Cheilocystidia*** 23–39 × 6–11 µm, fusiform, clavate to subcapitate at apex, wall thin and smooth, content homogeneous, hyaline, pale yellow to yellow brownish (4A3–5C7) in KOH. ***Caulocystidia*** not observed. ***Gill trama*** of parallel hyaline to yellowish white (4A2) hyphae in KOH and with smooth walls, the cells inflated, up to 23 µm in diam. ***Pileipellis*** a cutis of brownish yellow to light brown (5C8–5D5) hyphae 4.5–11 µm in diam., thin-walled, slightly incrusted to asperulate. ***Clamp connections*** present in all the tissues.

Habitat. Scattered on soil in broad-leaved forest in late autumn.

Additional materials examined. China. • Yunnan: Tengchong City, Yunfeng Mountain, on soil; 15 November 2019; Xiao-ming Zhang 37433 (HMJAU).

Discussion. Cylindrical basidiospores are uncommon in the genus *Pholiota*, making this species easily distinguishable from the others. In addition, it is readily recognized because of its dry pileus with slightly recurved and triangular scales and two types of pleurocystidia, including leptocystidia and chrysocystidia, as well as its growth on soil.

The stipe with multizonate squamules of this species reminds one of *Pholiota multicingulata* Horak, but the latter has smaller basidiospores (6.5–8 × 4.5–5 µm) and lacks chrysocystidia (Horak 1983).

Pholiota cylindrospora is similar to *P. squarrosa* (Vahl) P. Kumm. Both species have a dry pileus with obvious scales and two types of pleurocystidia: leptocystidia and chrysocystidia. However, the latter has smaller (6–7.5 × 3.8–4.5 µm) and elliptic basidiospores with a distinct germ pore and is wood-inhabiting (Smith and Hesler 1968; Holec 2001). *P. kodiakensis* A.H. Sm. & Hesler with two types pleurocystidia is also similar to *P. cylindrospora*; however, the former can be distinguished from the latter by its shorter spores (5–6 × 3–3.5 µm) and distinct germ pores with truncate apex (Smith and Hesler 1968). Furthermore, in the phylogram, *P. cylindrospora* clustered in the Subgenus *Pholiota* clade (Fig. 1). In this clade, this species was sister to *P. kodiakensis* and *P. squarrosa* with high statistical support (PP = 1, BS = 100), but represented a relatively independent lineage (Fig. 1). Therefore, it is proposed here as a new species belonging to *Pholiota* subgenus *Pholiota* based on morphological examination and phylogenetic analyses.

Pholiota subterrestris **E.J. Tian & J.H. Huang, sp. nov.**

MycoBank No: 854828

Figs 4, 5

Diagnosis. *Pholiota subterrestris* is distinguished from the other species of the genus *Pholiota* by brownish orange pileus with numerous brown fibrillose scales, pale brown and moderately broad lamellae with even edges, stipe covered with recurved fibrillose scales, evanescent fibrillose annulus; elliptic spores with distinct but small germ pore, fusoid ventricose pleurocystidia with typical amorphous refractive inclusion of chrysocystidia.

Figure 4. Basidiomata of *Pholiota subterrestris* (HMJAU37434, holotype). Photo by En-jing Tian. Scale bar: 1 cm.

Holotype. China. • Guizhou: Bijie City, Nayong County, Dapingqing National Wetland Park; elev. 1990 m; 26°41'10"N, 105°27'30"E; scattered on soil at base of stump; 22 July 2020; En-jing Tian 37434 (holotype: HMJAU!).

Etymology. The epithet *subterrestris* refers to the similarity to *Pholiota terrestris*.

Description. ***Pileus*** 10–35 mm in diameter, subhemispherical when young, with involute margin, slightly spread when mature, surface slightly viscid when wet, greyish orange to brownish orange (5B4–6C6), center dark, becoming paler towards the margin, covered with brown (6E7) fibrillose scales. ***Context*** thick, white to yellowish white (1A1–2A2), mild odor and taste. ***Lamellae*** decurrent to adnate or adnexed, moderately broad, close, L = 39–44, l = 3–7, pale yellow to light brown (4A3–5D6), edges even. ***Stipe*** 18–30 mm long, 4–7 mm thick, central, equal, solid, brownish orange (5C4) above, brown (6E5) below, covered with light brown (6D6) fibrillose squamulose, often compressed at the base

Basidiospores 5.4–6.1 × 3.6–4.2 µm, Q = 1.30–1.56, Q_m = 1.47, smooth, in face view broadly elliptic to elliptic, in profile a little bean-shaped, apical pore distinct but small, containing oil-bearing droplet or irregular inclusions, greyish yellow (4B5) in KOH and light yellow (4A5) in Melzer's reagent. ***Basidia*** 17.1–21.8 (–24.0) × 5.0–6.3 µm, 4-spored, clavate, hyaline in KOH, pale yellow (4A3) in Melzer's reagent. ***Pleurocystidia*** of two types: 1) 33.3–46.7 × 5.5–9.5 µm, subclavate to fusoid ventricose with a subacute apex, wall thin and smooth, content homogeneous, blond to dark yellow (4C4–4C8) to hyaline in KOH; 2) chrysocystidia, 34.2–58 × 8.3–10.4 µm, fusoid to fusoid-ventricose, the neck often drawn out to a crooked filamentose

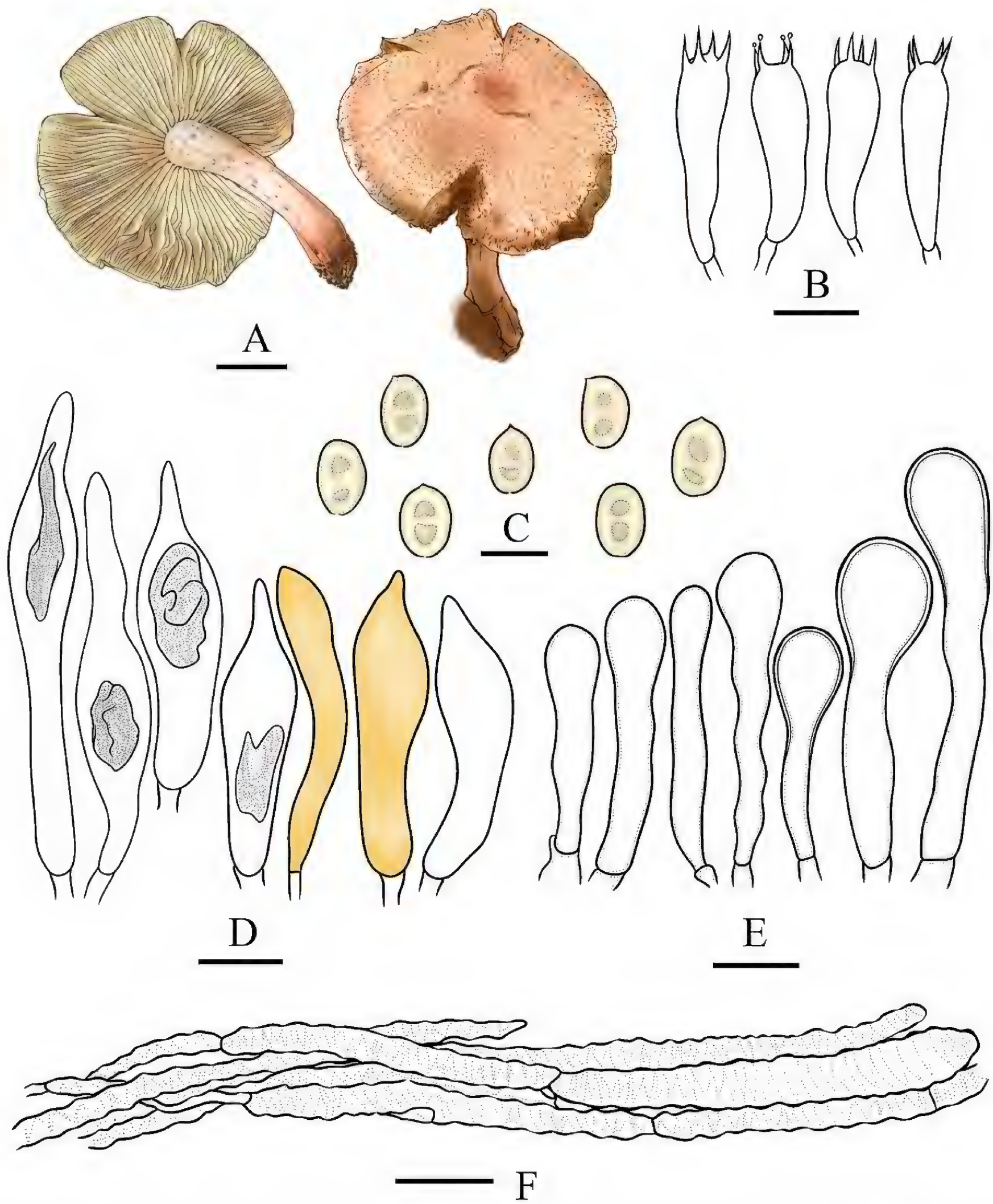

Figure 5. Microcharacters of *Pholiota subterrestris* (HMJAU37434, holotype). Drawings by Jia-hui Huang **A** basidiocarps **B** basidia **C** basidiospores **D** pleurocystidia **E** cheilocystidia **F** pileipellis. Scale bars: 1 cm (**A**); 5 µm (**C**); 10 µm (**B**, **D**, **E**); 20 µm (**F**).

projection with a subacute apex (up to 19.6 µm long), walls thin, smooth, with a refractive-amorphous inclusion, hyaline in KOH. ***Cheilocystidia*** abundant, (20.0–) 22.9–39.2 (–48.3) × 3.9–12.7 µm, clavate to clavate-capitate, wall thin, at times somewhat thickened in apex (about 1 µm), hyaline in KOH. ***Caulocystidia*** none observed. ***Gill trama*** of parallel hyphae, the cells inflated up to 27.5 µm, thin-walled, smooth, hyaline in KOH. ***Pileipellis*** hyphae hyaline to light brown (6D7), 3.7–10 µm diam., with encrusted walls. ***Content hyphae*** hyaline, 10–37.5 (–50) µm diam., cells inflated, smooth and thin-walled. ***Clamp connections*** present in all the tissues.

Habitat. Scattered or gregarious on soil at the base of a stump or on buried wood in summer.

Additional materials examined. China. • Guizhou: Bijie City, Qixingguan District, Baima Mountain, gregarious on soil or on buried wood, 15 August 2022, Guang-cheng Cao 37435 (HMJAU).

Discussion. This species is characterized by a brownish orange pileus with numerous brown fibrillose scales, pale brown lamellae with even edges, a stipe covered with recurved fibrillose scales, an evanescent fibrillose annulus, elliptic spores with a distinct but small germ pore, and fusoid ventricose pleurocystidia with typical amorphous refractive inclusions of chrysocystidia.

Pholiota subterrestris is similar to *P. terrestris* Overh., especially in terms of micro-characteristics, such as pleurocystidia, cheilocystidia, and basidiospores. However, it is easy to differentiate between the two species based on the macro characteristics. *P. terrestris* has a larger pileus (20–80 mm broad) without an orange tone, narrow and crowded lamellae with uneven edges, and a longer stipe (30–80 mm long) (Smith and Hesler 1968). Furthermore, in habitat, *P. terrestris* is caespitose on soil, whereas *P. subterrestris* is scattered or gregarious. Phylogenetic analyses showed that *P. subterrestris* was sister to *P. terrestris* in the Subgenus *Pholiota* clade (Fig. 1), which also indicated a close relationship between the two species.

Key to species of *Pholiota* Subgenus *Pholiota* from China

1 Pileus dry **2**
– Pileus viscid **4**
2 Spores cylindric, germ pore very minute to not evident ..... ***Pholiota cylindrospora* sp.nov.**
– Spores elliptic, germ pore distinct **3**
3 Spores 6–7.5 × 3.8–4.5 µm, germ pore apex not truncate ..... ***P. squarrosa***
– Spores 5–6 × 3–3.5 µm, germ pore apex truncate ..... ***P. kodiakensis***
4 Pileus ground color white to whitish ..... ***P. squarrosoides***
– Pileus ground color not white to whitish **5**
5 Spores 5–8 µm wide **6**
– Spores 2.5–5 µm wide **7**
6 Spores 6–8 µm wide, germ pore apex truncate ..... ***P. aurivelloides***
– Spores 5–6 µm wide, germ pore apex not truncate ..... ***P. aurivella***
7 Pileus with fibrillose scales **8**
– Pileus with spot-like or triangular scales **10**
8 Pileus and stipe brilliant yellow, spores smaller (4–5 × 2.5–3 µm) ..... ***P. flammans***
– Pileus darker, spores bigger (> 4.5 µm long, > 3.5 µm wide) **9**
9 Pileus 10–35 mm broad with orange tone, lamellae with even edges, stipe 18–30 mm long ..... ***P. subterrestris* sp.nov.**
– Pileus 20–80 mm broad without orange tone, lamellae with uneven edges, stipe 30–80 mm long ..... ***P. terrestris***
10 Spores 5–6 µm long ..... ***P. adiposa***
– Spores 6–8 µm long **11**
11 Lamellae whitish when young and becoming ferruginous ..... ***P. limonella***
– Lamellae yellow or pallid brownish when young **12**

12 Lamellae pallid brownish when young and becoming cinnamon, germ pore distinct ..... ***P. abietis***
– Lamellae yellow when young, germ pore minute or inconspicuous **13**
13 Stipe with appressed fibrillose scales, annulus persistent .... ***P. filamentosa***
– Stipe with recured floccose scales, annulus evanescent .... ***P. squarrosoadiposa***

Acknowledgments

We thank Shi-liang Liu, Guang-cheng Cao, and Xiao-ming Zhang for their contributions to the collection and photography of the specimens.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was funded by the National Natural Science Foundation of China (No. 31300017) and National Key Research and Development Program of China (2019YFC1604703).

Author contributions

En-jing Tian: conceptualization, resources, supervision, project administration, methodology, and funding acquisition. En-jing Tian, Jia-hui Huang, Chun-yu Lei, and Ya-lun Shen: investigation. Jia-hui Huang and Chun-yu Lei: software. Jia-hui Huang, Chun-yu Lei, and Ya-lun Shen: validation. Jia-hui Huang and Ya-lun Shen: data curation. En-jing Tian, Jia-hui Huang and Chun-yu Lei: visualization. En-jing Tian and Jia-hui Huang: formal analysis, writing-original draft preparation, and review and editing.

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Data availability

The research data used in this study can be found in GenBank (https://www.ncbi.nlm.nih.gov) and MycoBank (https://www.mycobank.org).

References

Bau T, Tian E, Wang H (2005) Strophariaceae of China (I) Pholiota. Journal of Fungal Research 3: 1–50. https://doi.org/10.13341/j.jfr.2005.03.001

Darriba D, Taboada G, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Molecular ecology 2: 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic biology 52: 696–704. https://doi.org/10.1080/10635150390235520

He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC, Raspé O, Kakishima M, Sánchez-Ramírez S, Vellinga EC, Halling R, Papp V, Zmitrovich IV, Buyck B, Ertz D, Wijayawardene NN, Cui B-K, Schoutteten N, Liu X-Z, Li T-H, Yao Y-J, Zhu X-Y, Liu A-Q, Li G-J, Zhang M-Z, Ling Z-L, Cao B, Antonín V, Boekhout T, da Silva BDB, De Crop E, Decock C, Dima B, Dutta AK, Fell JW, Geml J, Ghobad-Nejhad M, Giachini AJ, Gibertoni TB, Gorjón SP, Haelewaters D, He S-H, Hodkinson BP, Horak E, Hoshino T, Justo A, Lim YW, Menolli N, Mešić A, Moncalvo J-M, Mueller GM, Nagy LG, Nilsson RH, Noordeloos M, Nuytinck J, Orihara T, Ratchadawan C, Rajchenberg M, Silva-Filho AGS, Sulzbacher MA, Tkalčec Z, Valenzuela R, Verbeken A, Vizzini A, Wartchow F, Wei T-Z, Weiß M, Zhao C-L, Kirk PM (2019) Notes, outline and divergence times of Basidiomycota. Fungal Diversity 99: 105–367. https://doi.org/10.1007/s13225-019-00435-4

Holec J (2001) The genus Pholiota in central and western Europe. Vol. 20, IHW-Verlag, Munich, Bayern, Germany, 1–220.

Holec J, Kolařík M, Bizio E (2014) Pholiota chocenensis—a new European species of section Spumosae (Basidiomycota, Strophariaceae). Mycological progress 13: 399–406. https://doi.org/10.1007/s11557-013-0926-2

Horak E (1983) Mycogeography in the south Pacific region: Agaricales, Boletales. Australian Journal of Botany Supplementary Series 13: 1–42. https://doi.org/10.1071/BT8310001

Jacobsson S (1991) Pholiota in northern Europe. Winddahlia 19: 1–86.

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Dictionary of the Fungi 10th edn. CABI, Wallingford, England, UK, 1–771.

Kornerup A, Wanscher JH (1978) Methuen Handbook of Colour. Methuen, London, UK, 1–252.

Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30: 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Liu SL, Wang XW, Li GJ, Deng CY, Rossi W, Leonardi M, Liimatainen K, Kekki T, Niskanen T, Smith ME, Ammirati J, Bojantchev D, Abdel-Wahab MA, Zhang M, Tian E, Lu Y-Z, Zhang J-Y, Ma J, Dutta AK, Acharya K, Du T-Y, Xu J, Kim JS, Lim YW, Gerlach A, Zeng N-K, Han Y-X, Razaghi P, Raza M, Cai L, Calabon MS, Jones EBG, Saha R, Kumar TKA, Krishnapriya K, Thomas A, Kaliyaperumal M, Kezo K, Gunaseelan S, Singh SK, Singh PN, Lagashetti AC, Pawar KS, Jiang S, Zhang C, Zhang H, Qing Y, Bau T, Peng X-C, Wen T-C, Ramirez NA, Niveiro N, Li M-X, Yang ZL, Wu G, Tarafder E, Tennakoon DS, Kuo C-H, da Silva TM, Souza-Motta CM, Bezerra JDP, He G, Ji X-H, Suwannarach N, Kumla J, Lumyong S, Wannathes N, Rana S, Hyde KD, Zhou L-W (2024) Fungal diversity notes 1717–1817: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 124: 1–216. https://doi.org/10.1007/s13225-023-00529-0

Mao XL, Jiang CP (1993) Economic macrofungi of Tibet. Beijing Science and Technology Press, Beijing, China, 1–651.

Noordeloos ME (2011) Fungi Europaei, Volume 13: Strophariaceae s.l. Vol. 13, Edizioni Candusso, Alassio, Liguria, Italy, 1–648.

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Singer R (1962) The Agaricales in modern taxonomy. J. Cramer, New York, NY, USA, 1–915.

Singer R (1975) The Agaricales in modern taxonomy. J. Cramer, New York, NY, USA, 1–912.

Singer R (1986) The Agaricales in modern taxonomy. Koeltz Scientific Books, Koenigstein, Germany, 1–1069.

Smith AH, Hesler LR (1968) The North American species of Pholiota. Hafner Publishing Company, New York, NY, USA, 1–402.

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Tian E, Bau T (2004) Known Species of Pholiota (s.l.) from China and Their Distribution. Journal of Fungal Research 2: 25–34. https://doi.org/10.3969/j.issn.1672-3538.2004.01.003

Tian E, Bau T (2011a) New records of Pholiota collected from Changbai Mt. in China. Mycosystema 30: 408–413. https://doi.org/10.13346/j.mycosystema.2011.03.016

Tian E, Bau T (2011b) New Chinese records of Pholiota collected from Inner Mongolia and Heilongjiang. Mycosystema 30: 649–652. https://doi.org/10.13346/j.mycosystema.2011.04.023

Tian E, Matheny PB (2021) A phylogenetic assessment of Pholiota and the new genus Pyrrhulomyces. Mycologia 113: 146–167. https://doi.org/10.1080/00275514.2020.1816067

Tian E, Bau T, Ding Y (2016) A new species of Pholiota subgenus Flammuloides section Lubricae (Strophariaceae, Agaricales) from Tibet, China. Phytotaxa 286: 153–160. https://doi.org/10.11646/phytotaxa.286.3.2

Tian E, Gao C, Xie X, Zheng Y (2021) Stropharia lignicola (Strophariaceae, Agaricales), a new species with acanthocytes in the hymenium from China. Phytotaxa 505: 286–296. https://doi.org/10.11646/phytotaxa.505.3.4

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of bacteriology 172: 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols. Academic Press, San Diego, California, USA, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wu F, Zhou LW, Yang ZL, Bau T, Li TH, Dai YC (2019) Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. Fungal Diversity 98: 1–76. https://doi.org/10.1007/s13225-019-00432-7